A New Species of The Enigmatic Archosauromorph Doswellia from the Upper Triassic Bluewater Creek Formation, New Mexico, USA

By Andrew B. Heckert, Spencer G. Lucas, & Justin A. Spielmann

Abstract

Doswellia sixmilensis is a new species of the dos-welliid archosauromorph genus Doswellia named for an incomplete skeleton from the Upper Triassic Bluewater Creek Formation of the Chinle Group in west-central New Mexico, USA. D. sixmilensis differs from D. kaltenbachi Weems, the type and only other known species of Doswellia, in its larger size, higher tooth count and greater heterodonty, possession of keels on the cervical centra and the presence of discrete knobs or spikes on some osteoderms. The holotype of D. six-milensis is the fourth occurrence of Doswellia and only the second occurrence of a Doswellia skull, which includes the previously unknown premaxilla and maxilla (and therefore the best dentition) and has the best-preserved cervical vertebrae. Although it adds to our knowledge of the anatomy of Doswellia, this new information does not alter previous con-cepts of the phylogenetic relationships of the doswelliid gen-era, largely because they are so poorly known anatomically. The genus Doswellia is known from the Newark Supergroup in Virginia, and the Chinle Group in Texas, New Mexico and Utah, in strata of Otischalkian–Adamanian age. The type locality of D. sixmilensis is c. 43 m stratigraphically below a bed from which U-Pb dating of detrital zircons yields a maximum depositional age of c. 220 Ma, so this is a reasonable approximate numerical age for D. sixmilensis.

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Introduction

DURING the Triassic, archosauromorph diapsids underwent a dramatic diversification through which they evolved from a few endemic taxa into several speciose clades that would dominate nonmarine vertebrate ecosys-tems for the remainder of the Mesozoic (Fraser 2006; Sues and Fraser 2010). As part of this radiation, groups such as phytosaurs, aetosaurs and rauisuchians diversified widely and rose to become a common component of many Upper Triassic assemblages (Long and Murry 1995; Heckert and Lucas 2000; Brusatte *et al*. 2011; Nesbitt 2011). However, many other Late Triassic archo-sauromorph clades are only known from comparatively few individuals and, often, fragmentary material. Exam-ples include the silesaurids (Nesbitt *et al*. 2010; Kammerer *et al*. 2012) and the doswelliids (Desojo *et al*. 2011). As recognized by Desojo *et al*. (2011), the Doswelliidae con-sist of three genera (*Doswellia*, *Tarjadia* and *Archeopelta*), the latter two known only from fragmentary specimens. *Doswellia* itself is marginally better known, with multiple

specimens from the type locality (Weems 1980; Dilkes and Sues 2009) and fragmentary fossils identified from Texas (Long and Murry 1995) and, possibly, Utah (Parrish 1999). The occurrences from Texas and Utah are based on incomplete material, principally osteoderms, so the presence of *Doswellia* in the Upper Triassic of the American south-west has been open to question. Here, we document a new specimen consisting of an incomplete skull, a few cervical and, possibly, dorsal vertebrae and several osteoderms from the Upper Triassic Bluewater Creek Formation of New Mexico that represents a new species of *Doswellia*. This specimen simultaneously confirms that other specimens from the American south-west are referable to *Doswellia* and provides additional insight into the anatomy, diversity and distribution of the Doswelliidae.

de La Rioja, La Rioja, Argentina; TMM, Texas Memorial Museum, Austin; UCM, University of Colorado Museum, Boulder; USNM, United States National Museum of Natural History (Smithsonian), Washington, DC.

GEOLOGICAL SETTING

The fossils we describe are from NMMNH locality 5700 and were collected stratigraphically low in the Upper Triassic Bluewater Creek Formation (Chinle Group) in Sixmile Canyon, west-central New Mexico, USA (Fig. 1). The locality lies within the Cibola National Forest in McKinley County, and precise locality data are on file at the NMMNH (Fig. 1A–B). The fossils were found weathering from a purple mudstone unit immediately below the first prominent red band of Bluewater Creek Formation strata in Sixmile Canyon, in the middle of unit 4 of the Sixmile Canyon I measured section of Heckert and Lucas (2002*a*, 2003; Fig. 1C). The fossils themselves were scattered, with some vertebral fragments and osteoderms found weathered on the surface, and the remainder of the specimens were excavated in plaster jackets. All came from a relatively small area, with the *in situ* bones somewhat dispersed over a *c.* 2 × 2 m area in a blocky, relatively massive, somewhat bioturbated mudstone we interpret as a floodplain palaeosol deposit. Because of the small size of the specimens, most jackets were made 'blind', so no quarry map of fossil distribution exists. Importantly, none of the fossils were discovered earlier when one of us (ABH) prospected this area with NMMNH volunteers extensively as part of an earlier study (Heckert 1997*a*, *b*). Although there were a few other small fossils collected with the *Doswellia* specimens (including two limb bone fragments we describe here), all of the specimens we ascribe to *Doswellia* are consistent in size and morphology and are considered to represent the remains of a single individual. Furthermore, the osteoderms described here are relatively homogenous and clearly represent a single taxon and almost certainly a single individual. Importantly, these osteoderms were found in association with the cranial and postcranial elements described here, both loose on the surface and in jacketed material. The only other fossils recovered were a small stereospondyl centrum and an archosauriform tooth; the latter is too small and laterally compressed to have come from the jaws of the animal described here, and none of the fossils we describe as *Doswellia* bear any resemblance to stereospondyl elements. We are therefore confident that the fossils described here represent a single individual and almost certain that they represent a single taxon.

The Bluewater Creek Formation in west-central New Mexico has experienced intermittent palaeontological reconnaissance since Mehl *et al.* (1916), with the most

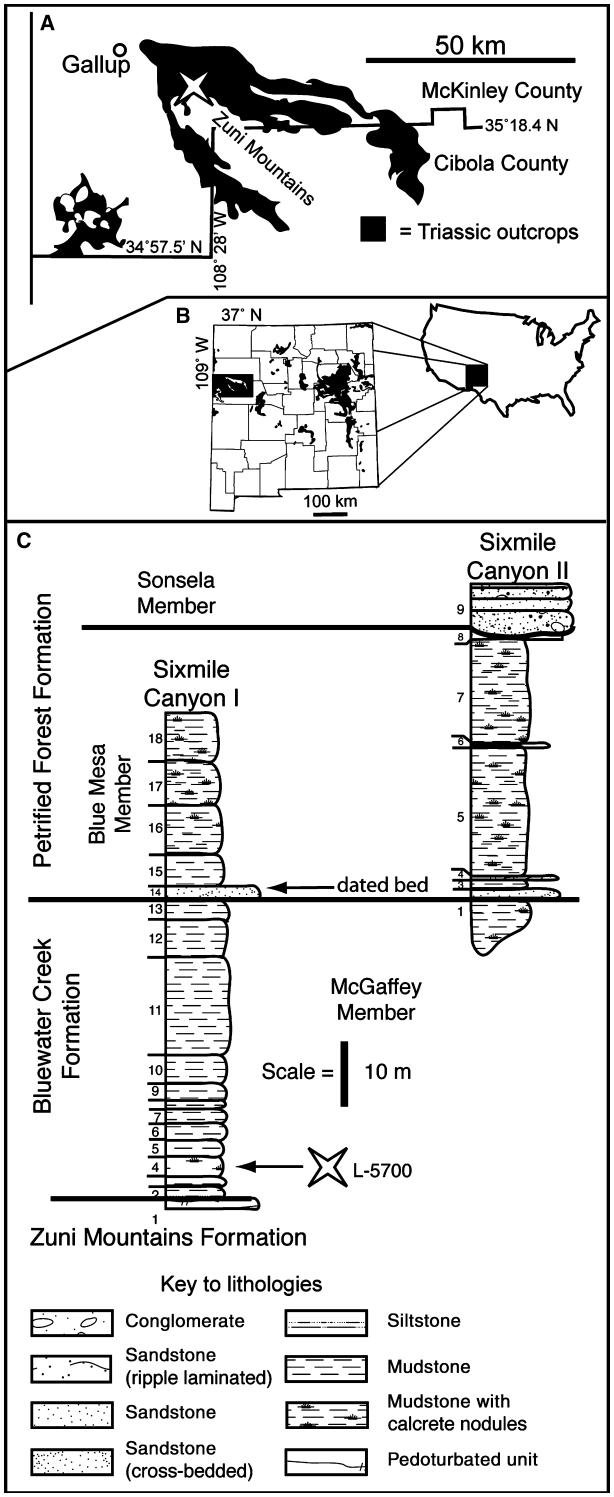


FIG. 1. Index map and measured sections of Upper Triassic strata in Sixmile Canyon, New Mexico, showing the geographic and stratigraphic position of the fossils described here. 'Dated bed' refers to the sandstone horizon sampled for detrital zircons reported by Irmis and Mundil (2008; Irmis *et al.* 2011) and Heckert *et al.* (2009).

recent reviews published by Heckert (1997*b*, 2004). In general, the Bluewater Creek Formation in the Sixmile Canyon area yields a typical Chinle Group tetrapod fossil assemblage of metoposaurid amphibians and a variety of archosaurs, principally phytosaurs and aetosaurs. Taxa diagnostic to lower taxonomic rank are rare, but include the aetosaurs *Stagonolepis* (= *Calyptosuchus*) *wellesi* and *Desmatosuchus haplocerus*, both index taxa of the Adamanian land-vertebrate faunachron (Lucas 1998, 2010). The microvertebrate assemblage documented by Heckert (2004) comes from a similar, or slightly lower, stratigraphic horizon low in the Bluewater Creek Formation and yields a relatively diverse assemblage of osteichthyans and tetrapods. Heckert (2004, table 11) indicated that this fauna included xenacanths, hybodontoids, redfieldiids, palaeoniscids, coelacanthids, the metoposaurs *Koskinonodon* (= *Buettneria)* and *Apachesaurus*, diverse archosauromorphs including aff. *Trilophosaurus jacobsi*, numerous archosauriform tooth morphotypes, phytosaurs and possible dinosaurs, including the putative ornithischian *Crosbysaurus harrisae*.

Since the description of the microvertebrates by Heckert (2004), there have been a few updates to the known fauna. Heckert *et al*. (2007) reidentified the incomplete osteoderm assigned to *Paratypothorax* by Heckert (1997*b*, fig. 3a–b), found as float approximately 150 m from the locality described here, as *Tecovasuchus* (Martz and Small, 2006). Irmis *et al*. (2007) considered 'ornithischian' taxa such as *Crosbysaurus* (reported by Heckert 2004) as valid taxa, but diagnostic only of Archosauriformes *incertae sedis*. More recently, Beatty and Heckert (2009) documented a large, pathological archosauriform tooth that could pertain to a phytosaur (as suggested by Heckert 1997*a*, *b*), but more likely represents a rauisuchian or other large archosaur from the same stratigraphic interval.

SYSTEMATIC PALAEONTOLOGY

Clade ARCHOSAUROMORPHA Huene, 1946
Family DOSWELLIIDAE Weems, 1980

Genus DOSWELLIA Weems 1980

Type species. Doswellia kaltenbachi Weems, 1980.

Diagnosis. Verbatim from Dilkes and Sues (2009, p. 59) for *Doswellia kaltenbachi*: Archosauromorph diapsid characterized by the following autapomorphies: elongate diapophyses of dorsal vertebrae with ventral concave and rugose surfaces for articulation with elongate capitulum of dorsal ribs; sharply angled cervical and anterior dorsal ribs; abrupt change in cross-sectional shape of ribcage from narrow to wide between anterior and posterior dorsal vertebrae; extensive series of osteoderms forming transverse rows from back of skull to at least base of tail and including at least five longitudinal rows on each side of vertebral column in posterior dorsal region; ilium with laterally deflected dorsal blade. *Doswellia* is also distinguished by the following unique combination of features: prominent occipital peg of supraoccipital that projects over dorsal rim of foramen magnum; euryapsid construction of temporal region with enlarged jugal below supratemporal fenestra; the absence of postparietals, tabulars and postfrontals; small elliptical supratemporal fenestra that does not reach occipital margin; squamosals with posteriorly directed 'horn-like' processes; elongate convex dorsal end of quadrate that fits into elongate ventral groove on squamosal; step between the flat skull roof and temporal region; the absence of lateral mandibular fenestra; teeth with slender, conical crowns lacking carinae; three sacral ribs, the first derived from dorsal region; pair of oval articular facets at distal tips of first two caudal ribs.

Remarks. With the discovery of the specimen we describe here, *Doswellia* comprises two species, the type species (*D. kaltenbachi* Weems) and the new species *D. sixmilensis*, named here. There is nothing in the new specimen that alters the diagnosis of the genus, although more complete materials may show that some of the features listed earlier do actually vary between the two species. Only the holotype and paratype specimens (see synonymies below) of *Doswellia kaltenbachi* can be referred to *D. kaltenbachi* with confidence. Other specimens in the literature, including the osteoderms from Texas identified as *Doswellia kaltenbachi* by Long and Murry (1995, p. 2, figs 19a–m, 20, 21) and those from an indeterminate archosauriform in Utah similar to *Doswellia* identified by Parrish (1999, p. 46, fig. 4), are best identified as *Doswellia* sp. (see discussion below). We note that the 'longitudinal rows' of osteoderms Dilkes and Sues (2009) referred to are best considered 'columns' of osteoderms *sensu* Heckert and Lucas (1999), who describe aetosaur carapaces in terms of longitudinal columns (parallel to the vertebral column) and transverse rows (often but not always one row per vertebral position). This convention can thus also be applied to the armour of nonaetosaurian archosauromorphs, as shown by Desojo *et al*. (2011), who also followed this terminology in their recent review of the Doswelliidae.

Doswellia kaltenbachi Weems, 1980

1980 *Doswellia kaltenbachi* Weems, 1980, pp. 3–53, figs 1, 7–25, pls 1–11, tables 2–9.
2009 *Doswellia kaltenbachi* Weems; Dilkes and Sues, p. 58, figs 1–15.
2011 *Doswellia kaltenbachi* Weems; Desojo *et al*., p. 161, fig. 16c, i.

Revised diagnosis. Species of *Doswellia* characterized by the absence of distinct knobs or protuberances on the osteoderms; also lacks ventral keels on the cervical centra. It may also be smaller and have a lower tooth count than the other species of *Doswellia*, *D. sixmilensis*, described below.

Doswellia sixmilensis sp. nov.
Figures 2–6

Derivation of name. Sixmile, as part of the type locality in Sixmile Canyon, and – *ensis*, meaning 'of' or 'from,' after the geographical region where the fossil was collected and to emphasize the specimens' proximity to the recently radioisotopically dated bed in Sixmile Canyon.

Holotype. NMMNH P-61909, an incomplete skeleton consisting of portions of the skull and lower jaws, several centra, and osteoderms, as well as two possible limb bone fragments.

Occurrence. NMMNH locality 5700, Sixmile Canyon, McKinley County, New Mexico.

Stratigraphic occurrence. Lower Bluewater Creek Formation, Chinle Group (Upper Triassic: Adamanian).

Referred material. The holotype is the only known specimen identifiable as *Doswellia sixmilensis*.

Diagnosis. Species of *Doswellia* distinguished from the type species, *D. kaltenbachi*, by a higher tooth count, a prominent ridge on the postorbital, the presence of keels on cervical centra and the presence of discrete knobs or spikes on some osteoderms. The holotype is significantly (50 per cent) larger than any known specimen of *D. kaltenbachi* and appears to exhibit greater heterodonty in tooth size, but the type series of both specimens are too incomplete to reliably compare. We note that many of the diagnostic characters of the genus as enumerated above by Dilkes and Sues (2009) are not preserved in the holotype of *D. sixmilensis* and discovery of more complete material will doubtless modify the generic diagnosis.

Description

The specimen we describe here, NMMNH P-61909, consists of many skull and lower jaw fragments, several fragmentary vertebrae, 13 complete and several fragmentary osteoderms and an assortment of miscellaneous rib and other unidentifiable bone fragments (Figs 2–5). The skull bones include portions of the left premaxilla (Fig. 2G–L), much of the right maxilla (Fig. 2A–F, O–Q), part of the left maxilla (Fig. 2M–N), an incomplete left postorbital and articulated parietal (Fig. 3K–N) and the right quadrate (Fig. 3A–F). The lower jaw is represented by the left surangular and articular (Fig. 3G–J) and a small fragment of the left angular (Fig. 3O–P). There is an isolated, but complete, tooth (Fig. 2R–S), found loose on the lower jaw elements but of uncertain position. The vertebrae include two relatively complete cervical centra (Fig. 4A–H) and several incomplete centra (Fig. 4I–W). Osteoderms range from relatively complete to fragmentary, but were found without association (Fig. 5). Associated elements that could pertain to the specimen include a distal left femur (P-61110) and an unusual girdle or ankle element (P-61111). Here, we describe the elements systematically, with the description of skull elements in the same order used by Dilkes and Sues (2009).

Premaxilla. A bulbous, tooth-bearing element approximately 7 cm long is interpreted as the tip of the left premaxilla (Fig. 2G–L). The proximal end is expanded, with four relatively large tooth sockets (Fig. 2J). As the element narrows, the tooth sockets become smaller, with the remaining four preserved sockets much smaller than the first four. There is room for approximately five more small tooth positions, but the bone is too poorly preserved to obtain an accurate tooth count. The first tooth position abuts the midline. The expanded 'bulb' is 2.3 cm across, with the narrower posterior portion only 1.9 cm across. Dorsally there is a smooth surface we interpret as the floor of the narial opening. Both the dorsal process and the posterior margin of the premaxilla are broken. In medial view, there is an extensive hollow between two ridges, one parallel to the tooth row and another at the level of the narial floor. Anteriorly, the bone is slightly more than 3 cm tall, which is taller than the anterior end of the maxilla described in the following paragraphs. Accordingly, we illustrate the premaxilla as if it were slightly downturned (Fig. 2I), as this is the condition in many other archosauromorphs. The external bone surface bears many coarser pits in addition to the minute nutrient foramina dorsal to the tooth row.

Maxilla. There are four fragments we interpret as portions of the maxillae of P-61909. Three are illustrated here, including two pieces of the right maxilla (Fig. 2A–F, O–Q) and one of the left (Fig. 2M–N). The fourth is a sliver of bone that preserves four tooth positions from the left maxilla, but very little else. We interpret a 6-cm-long piece bearing all or parts of 12 tooth sockets, six with broken teeth, as the anterior portion of a right maxilla (Fig. 2O–Q). Anteriorly, the bone is narrower, and the tooth positions are small and closely packed. Posteriorly, the bone widens, and there is one complete and one broken, much larger tooth socket (Fig. 2Q). In medial view, the palatal process appears to taper anteriorly, so we interpret this as the anterior portion of the right maxilla. We do not think the hollow is the Meckelian groove, which would make this fragment part of the left dentary. The smaller, anterior teeth appear to be firmly ankylosed to the jaw with swollen bone of attachment, the ankylothecodont condition of some authors (Chatterjee 1974; Sues 2003; Nesbitt 2011). Unfortunately, the dentition is not well enough preserved to permit further description of the teeth other than that they appear conical and are not obviously recurved or laterally compressed.

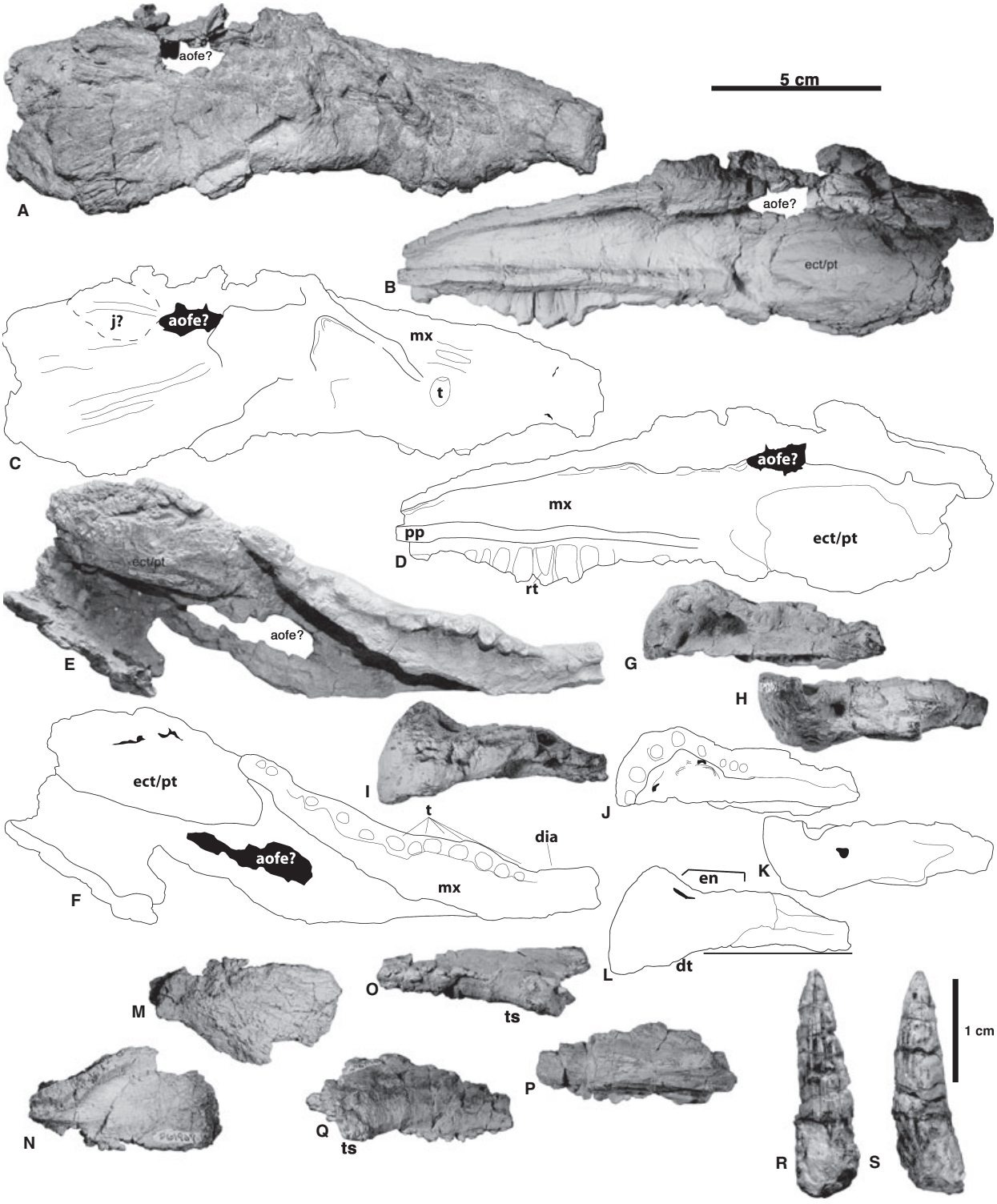
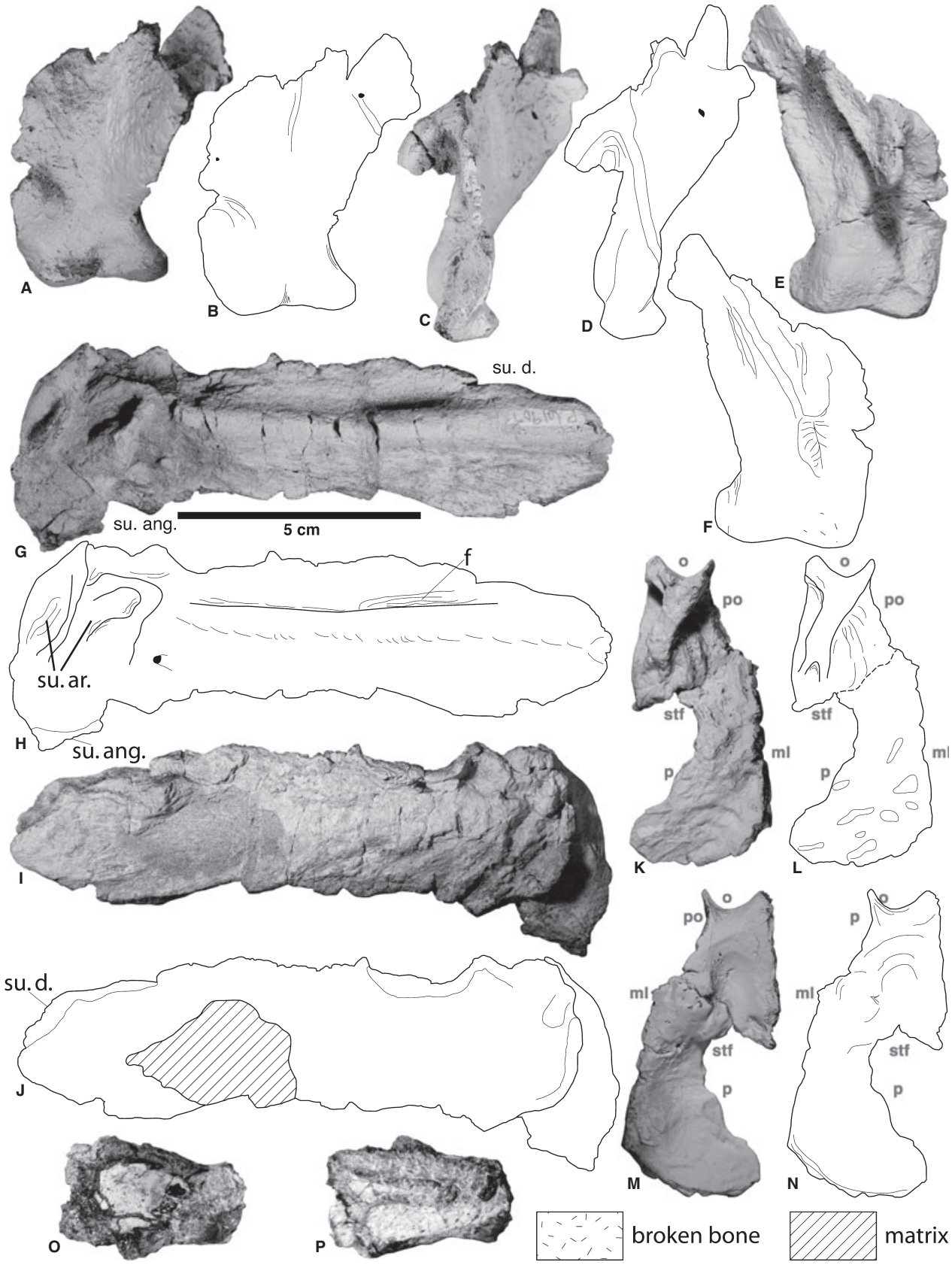


FIG. 2. A–S, photographs (A–B, E, G–I; M–S) and interpretive drawings (C–D, F, J–L) of the incomplete holotype skull (NMMNH P-61909) of *Doswellia sixmilensis* n. sp. from NMMNH locality 5700. A–F, right maxilla in A, C right lateral, B, D medial and E–F, ventral (occlusal) views. G–L, left premaxilla in G, J ventral, H, K dorsal and I, L, lateral views. M–N, left maxilla fragment in M, dorsal and N, ventral views. O–Q, dentulous right(?) maxilla(?) fragment in O, dorsal, P, ventral, and Q, lateral views. R–S, tooth in R, labial and S, lingual views. Abbreviations: aofe, antorbital fenestra; dia, diastema; dt, downturned margin of premaxilla (bar indicates level of tooth row); ect/pt, possible ectopterygoid or pterygoid fragment; en, external naris; j?, jugal(?) fragment; mx, maxilla; pp, palatal process of maxilla; rt, replacement tooth; t, tooth; ts, enlarged tooth socket. All scale bars represent 5 cm except R–S, 1 cm.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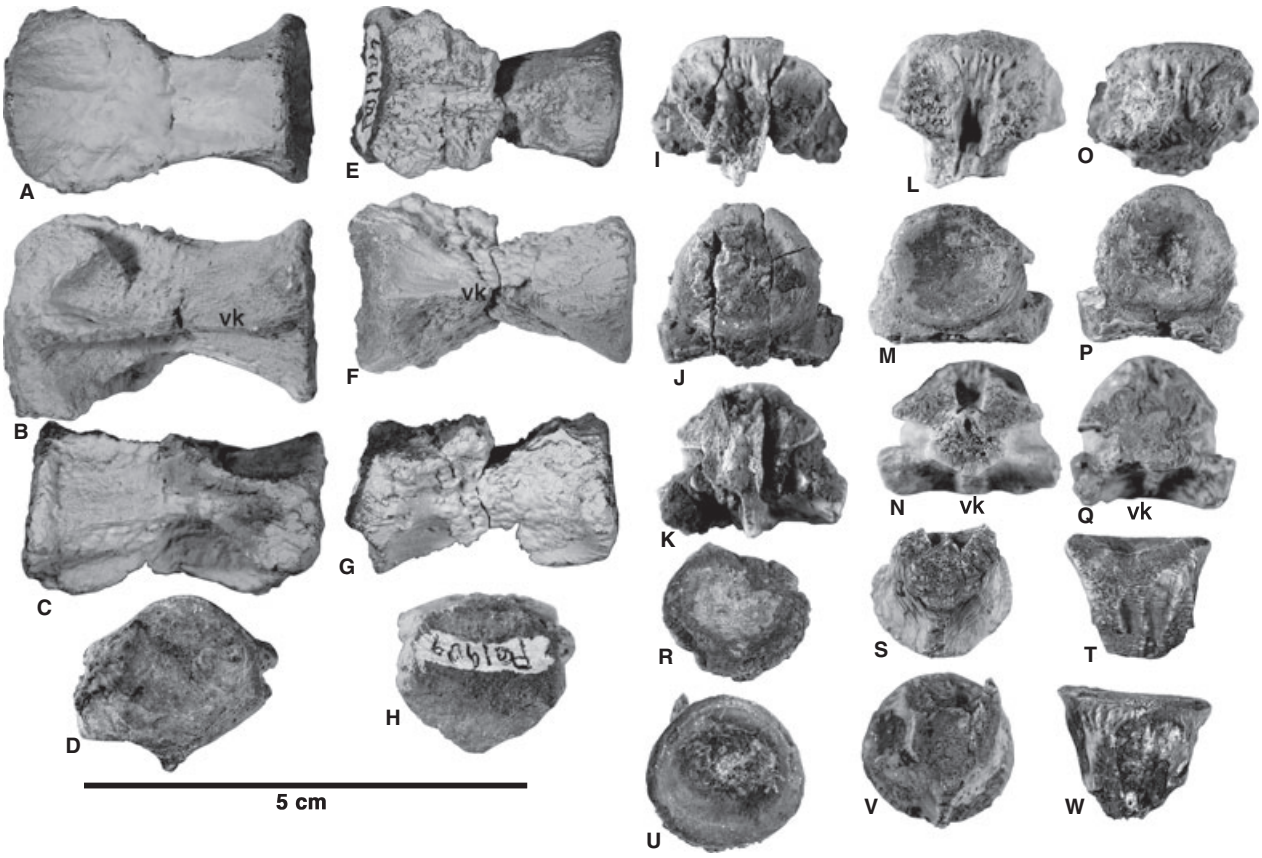

FIG. 4. Photographs of cervical and dorsal vertebral fragments of the holotype skeleton (NMMNH P-61909) of *Doswellia sixmilensis* n. sp. from NMMNH locality 5700. A–D, cervical centrum in A, dorsal, B, ventral, C, right lateral and D, articular views. E–H, cervical centrum in E, dorsal, F, ventral, G, right lateral and H, articular views. I–K, centrum fragment in I, dorsal J, anterior and K, cross-sectional views. L–N, centrum fragment in L, dorsal, M, anterior and N, cross-sectional views. O–Q, centrum fragment in O, dorsal, P, anterior and Q, cross-sectional views. R–T, dorsal centrum fragment in R, anterior, S, cross-sectional and T, dorsal views. U–W, dorsal centrum fragment in U, anterior, V, cross-sectional and W, dorsal views. Abbreviation: vk, ventral keel. Scale bar represents 5 cm.

The largest bone fragment associated with P-61909 is approximately 18 cm long and consists primarily of the right maxilla. The bone is long and low, as little as 1.8 cm tall anteriorly and only *c.* 5.2 cm tall posteriorly and is only slightly crushed (Fig. 2A–F). The anterior end is narrow, then bulges laterally for approximately seven tooth positions, narrows slightly and then gradually widens for the remainder of the 20 total tooth positions (Fig. 2E–F). All tooth positions posterior to the bulge are slightly, but noticeably, smaller than those in the bulge. There may be a very short diastema anterior to the expansion. In lateral view, the external texture is extremely rugose and consists primarily of strongly developed grooves and ridges, most of which trend approximately anteroposteriorly. A prominent ridge runs dorsomedially from the bulge to an opening we interpret as the anterior margin of the antorbital fenestra (Fig. 2A–C). The bone surrounding the antorbital fenestra is crushed and distorted, but the anterior margin is thickened, and posteriorly the bone appears less thick. As preserved, there is a thin bridge of bone and matrix that appears to close off the antorbital fenestra dorsomedially (Fig. 2A–F), but this may be an artefact of crushing, and the opening may have been larger in life. Posteriorly, some of the grooved bone appears slightly displaced and may actually represent the anterior edge of the jugal, but no unambiguous sutures or bone margins are discernable. In medial view (Fig. 2B, D), the palatal process is distinct, but relatively narrow and tapers posteriorly. The medial edge of the maxilla appears

FIG. 3. Photographs (A, C, E, G, I, K, M, O–P) and interpretive drawings (B, D, F, H, J, L, N) of the incomplete holotype skull and mandible (NMMNH P-61909) of *Doswellia sixmilensis* n. sp. from NMMNH locality 5700. A–F, quadrate in A–B, anterior, C–D, lateral and E–F posterior views. G–J, left surangular in G–H, medial and I, J lateral views. K–N, skull roof fragment in K–L, dorsal and M–N, ventral views. Abbreviations: f, foramen; ml, midline; o, orbital margin; p, parietal; po, postorbital; stf, supratemporal fenestra; su. ang., suture with angular; su. ar., suture with articular; su. d., suture with dentary. Dashed line indicates inferred suture. Scale bar represents 5 cm.

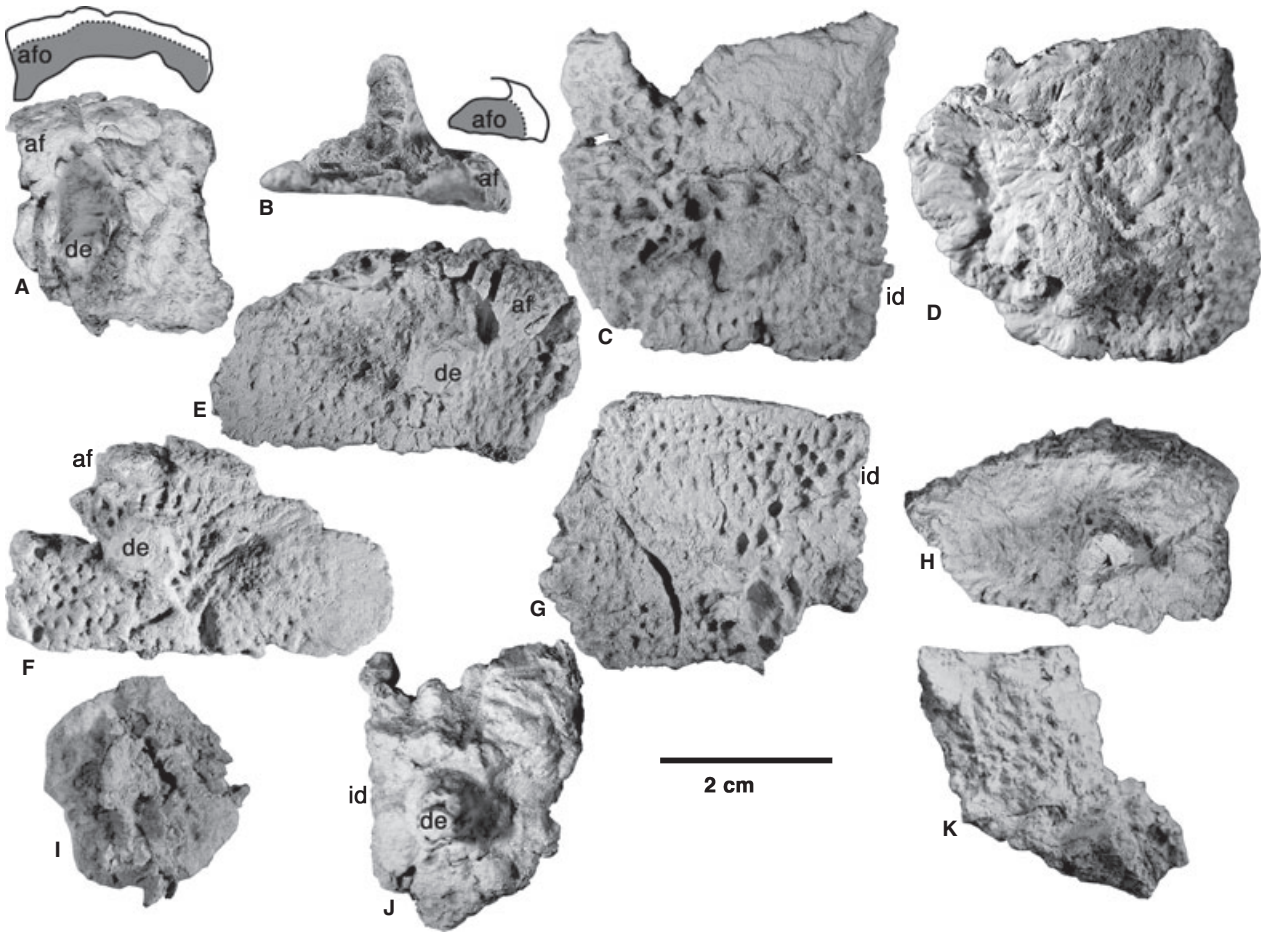

FIG. 5. Osteoderms of the holotype skeleton (NMMNH P-61909) of *Doswellia sixmilensis* n. sp. from NMMNH locality 5700. A–B, spinose osteoderm in A, dorsal and B, lateral? view (sketches show overlap of articular facet). C–K, various osteoderms in dorsal view including E, left lateral side of nuchal element and F, right side of nuchal element. All osteoderms oriented with anterior towards the top of the page. Abbreviations: af, articular facet; afo, shaded area overlapped by articular facet; de, dorsal eminence; id, interdigitating articulation of another osteoderm in the same row. Scale bar represents 2 cm.

intact dorsally, preserving a narrow space for the posterior projection of the nasals. A large, rounded mass of bone and underlying matrix on the posterior portion of the element may be the ectopterygoid or lateral portion of the pterygoid, but is poorly preserved and indistinct, hence the tentative identification on the figures (Fig. 2B, D–F).

Postorbital. The only identifiable portion of the skull table is a 6.4-cm-long fragment preserving parts of the left postorbital and parietal (Fig. 3K–N). A small gap along the anteromedial margin presumably held the frontal, so we consider the presence of a postfrontal unlikely. Anteriorly, the element has a prominent ridge that forms part of the posterior margin of the orbit. This ridge is much better developed than the flexed surface illustrated in *Doswellia* by Dilkes and Sues (2009, fig. 1a). The lateral margin is incomplete, but there is no indication of an infratemporal fenestra. The exact juncture with the parietal is indistinct but appears to be at the anteromedial edge of the supratemporal fenestra, which is bounded anteriorly by the postorbital.

Parietal. The parietal is thin and flat, with well-developed pits adorning the dorsal surface (Fig. 3K–N). The midline suture is well preserved, as is the lateral margin, much of which bounds the supratemporal fenestra medially. The lateral surface that articulates with the overlapping portions of the squamosal is well preserved, albeit slightly chipped and thus more irregular in appearance than it was in life. The posteromedial extension is broken, so the posterior margin appears less embayed than in the illustration of *Doswellia kaltenbachi* by Dilkes and Sues (2009, fig. 1a). It appears that the supratemporal fenestra is much broader anteriorly and tapers posteriorly.

Quadrate. The right quadrate is complete and one of the best-preserved bones available, lacking only a small piece of the condyle and some edges of thinner sheets of bone (Fig. 3A–F). This element matches Dilkes and Sues' (2009, fig. 1b, c) illustrations almost perfectly, but is more difficult to reconcile with Weems' (1980, fig. 11) illustration. The quadrate is a complex element, lacking a quadrate foramen (as noted in the holotype of *D. kaltenbachi* by Dilkes and Sues 2009). The anteromedially project-

ing sheet of bone bears two longitudinal ridges medially, one extending from near the medial condyle anterodorsally just dorsal to the ventral margin. A second, less pronounced ridge parallels the first but lies near the dorsal margin of the bone and supports the posterior projection. The articular surface is, in ventral view, composed of two broad, connected condyles and is strongly concave anteriorly and weakly concave posteriorly, so that the articular is strongly buttressed anteromedially and somewhat less so laterally. The articular surface is at least 2.3 cm across, but as much as 2.9 cm across its maximum lateral to maximum medial extent.

Surangular. A nearly complete, but weathered, left surangular is included in P-61909 (Fig. 3G–J). Dilkes and Sues (2009) described in detail this element in the holotype of *D. kaltenbachi*, so we provide only a few additional details, highlighting slight differences based on the specimen described here. As preserved, it is *c.* 13 cm long and superficially appears more rectangular in lateral view, but this is at least partially an artefact of breakage along its ventral margin. The ornamentation on the lateral side is well developed and consists of elongate pits and short ridges posteriorly. Anteriorly, the surface is badly weathered. In medial view, it well matches the same element illustrated by Dilkes and Sues (2009, fig. 2a–d). As noted by Dilkes and Sues (2009), the articulation for the quadrate is complex and bounds the lateral margin of the jaw joint. A small portion of the angular is present along the ventral margin of the posterior end of the element.

Articular. The left articular was preserved in close association with the surangular (Fig. 3O–P). It is subrectangular, with a maximum length slightly less than 4 cm and breadth approximately 2.4 cm. it is heavily concreted, but generally conforms to the descriptions and illustrations of Dilkes and Sues (2009, fig. 2g–h). The retroarticular process, as they note, is subrectangular and would largely be obscured in lateral view. We note that the bone comprising the retroarticular process is also extremely thin. The articular surface is quadrilateral, almost square, and is much narrower (*c.* 1.3 cm) than the 2.3-cm-wide articular surface of the quadrate.

Dentition. One isolated tooth (Fig. 2R–S) was found with the left surangular and articular, and the morphology of preserved *in situ* tooth fragments is sufficiently similar that we think it represents a tooth of *Doswellia*. The tooth is relatively tall (2.3 cm), narrow, and circular (*c.* 0.6 cm diameter) in cross-section (Fig. 2R–S). The crown is extremely weakly recurved and possesses many longitudinal striations that radiate basally from the tip. Much of the enamel is stripped off, but there is no indication of serrations or denticles of any kind. It lacks a ridge that would have supported a carina, a feature often seen in enamelless teeth found in the Chinle (Heckert, 2004). Its size is consistent with the larger teeth seen in the bulges of the premaxilla and maxilla. Smaller teeth appear similar, consisting of relatively simple, conical to very weakly recurved, peg-like cones that are essentially circular in cross-section, are not laterally compressed and have baso-apical longitudinal striations or fluting.

The medial portion of the right maxilla reveals several replacement teeth in the labial bulge (Fig. 2B, D). These teeth are lingual (medial) to the crowns they replace and have nearly resorbed most of the roots of the existing dentition. The best-preserved crown appears more conical and sharply pointed.

Vertebrae. Two relatively complete centra and five half centra preserving articular facets are present (Fig. 4). The two complete centra are both cervicals (Fig. 4A–H), as are the three preserved anterior halves (Fig. 4I–Q), because all of these elements have prominent parapophyses low on the body of the centrum. The two posterior halves (Fig. 4R–W) are probably also cervicals, based on the presence of a ventral keel. The absence of neural arches strongly implies that the individual was not a fully ossified adult and was therefore still skeletally immature (Irmis 2007).

There are several striking features of these centra. They are somewhat unusual in that they are relatively low and broad, with articular facets that are slightly wider than tall (a feature noted by Dilkes and Sues 2009). The parapophyses are proportionately large and extend below the ventral margin of the articular facet. In anterior view, the parapophyses form broad shoulders (rounded bulges) that extend across the ventral margin of the articular facet and meet the prominent ventral keel at the midline (Fig. 4D, H, J–K, M–N, P–Q). The parapophyses themselves are ovoid, longer than dorsoventrally tall and directed laterally to somewhat ventrally. In cross-section, the vertebrae are especially striking as the convergence of the articular facets, the diapophyseal portion of the neural arch, and the parapophyses near the middle of the centrum creates an x-shaped, or cruciform, cross-section, with narrow, yet deep hollows between the parapophyses and the neural arch, best seen in the broken cervicals (Fig. 4K, N, Q), but also apparent when examining the two more complete vertebrae. No diapophyses are preserved, but there are huge facets on the cervical centra for the articulation of the neural arches. These take the form of broad surfaces that extend laterally beyond the margin of the articular face. The neural canals are deeply excavated, extending below the dorsal margin of the articular facets. In some centra, the ventral surface of the canal (dorsal surface of the centrum *sensu stricto*) is ornamented by three low keels or striations descending from the anterior edge onto the floor of the canal (Fig. 4I, K–L, N–O, Q).

Osteoderms. There are 13 complete or reasonably complete osteoderms and numerous osteoderm fragments associated with NMMNH P-61909, the holotype of *Doswellia sixmilensis* (Fig. 5). Four of these osteoderms were found with the quadrate in close association with each other and may correspond to the 'nuchal element' described by Weems (1980) and Dilkes and Sues (2009). Although they are neither complete nor articulated, some (Fig. 5E–F) are less quadrilateral and more strongly tapered laterally than others. Five more osteoderms were found in the jacket with the lower jaw elements, and the rest were isolated, or at least not closely associated with other elements. All are relatively small (less than 50 mm maximum dimension, typically less than 30 mm), relatively uniform in thickness and ornamentation and therefore are considered to represent elements of the holotype of *Doswellia sixmilensis*, NMMNH P-61909.

The osteoderms of NMMNH P-61909 are generally quadrilateral, but much less regular than those of aetosaurs or the cruro-

tarsan *Revueltosaurus* (Long and Murry 1995; Heckert and Lucas 2000; Parker *et al*. 2005), yet proportionately thinner and more polygonal than phytosaur osteoderms. They also lack the anterior projections that typify sphenosuchian osteoderms or the elaborate spines of the enigmatic archosauriform *Euscolosuchus olseni* Sues (Sues 1992). All are relatively small and most are approximately square, with only a few that are definitively wider than long or longer than wide. In general, their length is comparable with that of the preserved centra, so that there may have been one row of osteoderms for each of the vertebrae, a feature seen in many (but not all) aetosaurs (Long and Murry 1995; Heckert and Lucas 2000).

The dorsal surface bears an ornamentation of dense, relatively deeply incised, pits. These pits are much more densely packed than in other Triassic tetrapods, particularly phytosaurs and aetosaurs (Long and Murry 1995), with the possible exception of the putative aetosaur *Acaenasuchus* (Long and Murry 1995; Heckert and Lucas 2002*b*) but are characteristic of *Doswellia kaltenbachi* (Weems 1980; Dilkes and Sues 2009). Where they differ from *D. kaltenbachi* is in the presence of a pronounced dorsal eminence, or spine, emanating from a point near the centre or slightly medial to the centre of some osteoderms (Fig. 5A–B, E–H). This spine is often broken, but in the best-preserved specimens clearly projects several millimetres (more than half the width of the osteoderm) above the osteoderm. Several of the other osteoderms (Fig. 5C–D) possess a lower, anteroposteriorly longer knob or keel. Only a few of the recovered osteoderms (Fig. 5C, G, J) possess clear articulations with other osteoderms in the same row. These articulations were described as 'tongue-and-groove' by Long and Murry (1995) but are better described as 'interdigitating' with osteoderms lateral and/or medial to them. This is probably at least in part an artefact of preservation, as the edges of the osteoderms are thin and brittle.

Of the osteoderms found in the same jacket as the quadrate, some are sutured together (Fig. 5E–F) and may represent part of the 'nuchal element' described by Dilkes and Sues (2009) in *Doswellia*. Preservation is not good, but each appears to consist of a larger (20–25 mm wide, 29–31 mm long) element articulated with a shorter, more rounded lateral element. We thus interpret the osteoderm in Figure 2E as from the left side and that in Figure 2F from the right. The spine is located slightly towards the lateral side of the more medial osteoderm. The two specimens do not articulate at the midline, so there may have been other osteoderms incorporated into the nuchal element.

A few of the osteoderms also possess an unusual articulation on the anterior portion of the dorsal surface (Fig. 5A–B, E–F). Although many have a slightly smoother surface reminiscent of the anterior bar or anterior lamina of various aetosaurs (Long and Ballew, 1985; Heckert and Lucas, 2000), the specimens highlighted here possess a similar facet that actually projects posterodorsally over the ornamented portion of the osteoderm, a feature we have not observed in any other Triassic tetrapod (Fig. 5A–B).

Appendicular elements. Two incomplete elements, interpreted here as a distal left femur and a possible calcaneum, were found in the assemblage. Because the appendicular skeleton of *Doswellia* is essentially unknown, and because the ankle element appears too large relative to the femur, these elements were catalogued separately, even though one or both may well pertain to *Doswellia*.

The distal femur is only 19 mm long, with a maximum breadth of 27 mm. Its form is somewhat generalized, with the lateral condyle larger than the medial, but projecting only slightly more distally. A distinct sulcus lies on the lateral surface, where it is bounded distally and posteriorly by the articular surface. There is a faint constriction between the larger lateral and smaller medial condyle. Like the lateral condyle, the medial condyle has a slight posterior projection that bounds a small sulcus on its medial side.

The ankle element possesses a large, triangular, rounded face, with one smooth articular surface and the other surfaces somewhat rougher. A flange of bone runs from these surfaces across the long axis of the element, but it is broken off, so its original height is unclear. It terminates in a small rounded surface, so this may be a primitive calcaneal tuber.

COMPARISONS

Because of the fragmentary nature of most doswelliid fossils, the osteoderms we described here are actually the focus of most of our comparisons. Where possible, we have compared other elements, primarily the skull (to *Doswellia*) and the vertebrae (across many taxa), but the bulk of the comparisons must lie with the osteoderms as they are the shared elements known from NMMNH P-61909 and the doswelliids *Doswellia*, *Tarjadia* and *Archeopelta*.

As documented in the preceding description, the osteoderms of NMMNH P-61909 possess an ornamentation of coarse, relatively deeply incised, subcircular to circular pits and an unornamented anterior lamina (articular surface), unambiguous synapomorphies of Doswelliidae (Desojo *et al*. 2011). Among other contemporaneous archosauromorphs with osteoderms converging on those of doswelliids, these osteoderms differ from both *Euscolosuchus* (Sues 1992) and *Acaenasuchus* (Long and Murry 1995; Heckert and Lucas 2002*b*) in being considerably less spinose. The pitting on these osteoderms, however, is also more dense and regular than in *Acaenasuchus*, so we accept them as doswelliid.

Within Doswelliidae, the osteoderms of NMMNH P-61909 are much more similar to *Doswellia* than to *Archeopelta* or *Tarjadia*. In particular, the pattern of pitting is very dense and composed of strongly incised subcircular pits in an otherwise thin osteoderm (e.g. Desojo *et al*. 2011, fig. 16g–i). In *Tarjadia*, the pits are proportionately larger, less densely packed, bear a more clearly radial pattern, and the osteoderms, themselves, are proportionately thicker, up to 20 per cent of their length (Arcucci and Marsicano 1998; ABH pers. obs. of casts of PULR 063). The osteoderms bear a dense pattern of finer pitting (>10

pits across the transverse width) than seen in *Archeopelta* (*c*. 8, see Desojo *et al*. 2011, fig. 13c, 16g–i). Known osteoderms of *Archeopelta* also lack a keel or eminence, a feature that is apparent on *Doswellia kaltenbachi* (Weems 1980; Dilkes and Sues 2009) and is carried to an extreme with a spine in some osteoderms of NMMNH P-61909. The osteoderms of NMMNH P-61909 are also thinner than the relatively thick osteoderms (thickness approximates 20 per cent total osteoderm length) seen in 7 mm thick, *c*. 30 × 37 mm *Archeopelta* osteoderms (Desojo *et al*. 2011, table 5).

Thus, the osteoderms of NMMNH P-61909 are not only doswelliid, they most closely resemble those of *Doswellia,* itself. In particular, they are similar in size, shape, thickness and density and pattern of pitting. The primary difference is that, although *D. kaltenbachi* is known to have keeled osteoderms, at least some of the osteoderms of P-61909 have a prominent conical, spine-like dorsal eminence.

If we limit our analysis to existing phylogenies, there are no other character states exhibited by NMMNH P-61909 that justify explicit referral to the genus *Doswellia*. However, we feel that the extreme similarity of many elements, in particular the quadrate and surangular, as well as the similarity in osteoderms and cervical vertebrae, justify our assignment of NMMNH P-61909. In the following paragraphs, we highlight these similarities.

Although there are no characters of the quadrate expressly used to diagnose *Doswellia*, or even doswelliids generally, the strong resemblance of this complex element to that of *Doswellia* is striking. In particular, we note the absence of a quadrate foramen as well as the overall size and shape. Indeed, the only difference we find is that in posterior view the processes are less sinuous than in *Doswellia kaltenbachi* as illustrated by Weems (1980, fig. 10) and Dilkes and Sues (2009, fig. 1c); otherwise, this element is identical.

Similarly, the surangular is an almost exact match for the surangular of *Doswellia*. The only differences we note are that the foramen ventral to the longitudinal ridge in *Doswellia kaltenbachi* is located more dorsally, on the ridge, in P-61909, and the groove on the lateral surface is less well developed. Because of the narrow articular surface on the articular, the surangular makes a substantial contribution to the jaw articulation with the quadrate, as it does as in the type specimen of *Doswellia kaltenbachi* (Weems 1980; Dilkes and Sues 2009).

The separate tooth (Fig. 2R–S) is only weakly recurved but prominently striated. The striations give it a fluted appearance similar to that seen in many unserrated phytosaur teeth (Hunt 1989; Hungerbühler 2000), and it is also superficially similar to the larger teeth of metoposaurs and other temnospondyls. However, it is not labyrinthodont, ruling out stereospondyl affinities, and it is less recurved than most phytosaur teeth, additional reasons that we suspect that it represents a tooth of *Doswellia*. Dilkes and Sues (2009) describe no striated teeth, but Weems (1980) refers to several 'fluted teeth' among those found with the type specimen of *D. kaltenbachi*. As mentioned previously, the tooth is consistent in size and shape with the larger tooth sockets in the maxilla and premaxilla. Dilkes and Sues (2009) consistently describe the teeth of *Doswellia* as recurved, but it is apparent from their illustrations that the recurvature is minimal, at least compared with contemporaneous archosaurs such as phytosaurs and rauisuchians.

A few other comparisons are noteworthy. Although the parietal in NMMNH P-61909 appears to lack a straight-line contact with the squamosal, this portion of the bone is not well preserved. The squamosal would overlap that surface (Dilkes and Sues 2009), which could give the appearance of a straight-line contact regardless of the parietal's shape, so this is probably not taxonomically significant.

There is no convincing connection of the premaxilla and maxillary fragments. Thus, the estimate of *c*. 42 tooth positions preserved in these elements is an underestimate of the total number. Given the small size of many of the teeth, we suspect that there were at least 50 and perhaps more tooth positions in each side of the upper jaws. This is many more than the 35 indicated in the referred dentary described by Weems (1980; Dilkes and Sues 2009), but the latter element is not well preserved, and archosauromorphs often have contrasting numbers of teeth in their upper and lower jaws. The heterodonty in tooth size we document here is also much greater than the slight decrease in size documented in the posterior tooth positions of the referred mandible of *Doswellia kaltenbachi* described by Weems (1980) and Dilkes and Sues (2009).

Unlike *Doswellia kaltenbachi* (Weems 1980; Dilkes and Sues 2009), we find the ventral keel in the cervical centra to be very prominent, extending along the length of the centrum and, where complete, actually extending farther ventrally than the ventral margin of the articular face (Fig. 4B–C, F–G, K, N, Q). Keeled cervical centra are widely distributed throughout Archosauromorpha, so this appears to be simply a species-level difference within *Doswellia*.

DISCUSSION

As enumerated in the differential diagnosis, there are several significant differences between the holotype of *Doswellia sixmilensis* and *D. kaltenbachi*. Specifically, *D. sixmilensis* possesses a higher tooth count, a prominent ridge on the postorbital, keels on the cervical centra and discrete knobs or spikes on some osteoderms. It also is

larger and appears to possess greater heterodonty in tooth size. In the light of these differences, it is reasonable to wonder if NMMNH P-61909 in fact represents a genus distinct from *Doswellia*. In the present study, we have taken what we feel is a conservative approach, noting the extremely similar morphology of some skull elements as well as the osteoderms (and, to a lesser extent, the cervical centra) of NMMNH P-61909 and previously described specimens of *Doswellia*.

Much of the skull morphology we document here is new, especially that of the premaxilla and maxilla. Thus, we are able to establish several features not previously recorded by previous authors, allowing us to modify Weems' (1980, figs 8–9, 12) necessarily speculative reconstructions of the skull as well as updating the character codings used by Dilkes and Sues (2009) and, subsequently, by Desojo *et al.* (2011; Fig. 6).

Regarding Weems' (1980) reconstructions of the skull, we document several features that are completely different. These include a much more rostral position of the external nares, the downturned 'bulb' of teeth at the tip of the rostrum, lateral expansions or bulges in the maxillary tooth row and the presence of an antorbital fenestra (Fig. 6). This results in a much more complex skull outline. This pattern superficially resembles that seen in some phytosaurian taxa, but even the most heterodont phytosaurs (Hungerbühler 2000) lack the dramatically different-sized teeth in the maxillary dentition of *Doswellia* we describe here. *Doswellia* possesses a well-developed pattern of heterodonty in tooth size in the upper dentition, with substantially larger teeth in the lateral bulges and much smaller teeth in the intervening spaces. The complex tooth row shape we document is not reflected in the referred mandible described by Weems (1980; Dilkes and Sues 2009), which has an essentially homodont dentition. However, despite the differences in tooth size and tooth row shape, the preserved dentition is similar between P-61909 as described here and the type and referred specimens of *D. kaltenbachi* (Weems 1980; Dilkes and Sues 2009). We note that the morphology of the snout of *Doswellia* is distinct from that of phytosaur snouts, which they superficially resemble. In particular, the rostral end (premaxilla) is more hollow, and the dentition is much more strongly heterodont in *Doswellia* (Fig. 6).

Beyond the relatively minor difference of ventrally keeled cervical centra in *D. sixmilensis* relative to the unkeeled centra of *D. kaltenbachi*, the most significant difference between the two species we see in the highly diagnostic postcrania are the spiny osteoderms of *D. sixmilensis*. Neither Weems (1980) nor Dilkes and Sues (2009) describe or illustrate spinose osteoderms in *D. kaltenbachi*. Long and Murry (1995) note that osteoderms they referred to *D. kaltenbachi* usually possess longitudinal keels bearing the same pattern of fine pits, but that these keels are 'never sharp', even on the lateral osteoderms (Long and Murry 1995, p. 30). However, the ridge on at least one of the specimens they illustrate (Long and Murry 1995, fig. 21e–f) is tall enough to resemble a spine like those illustrated here.

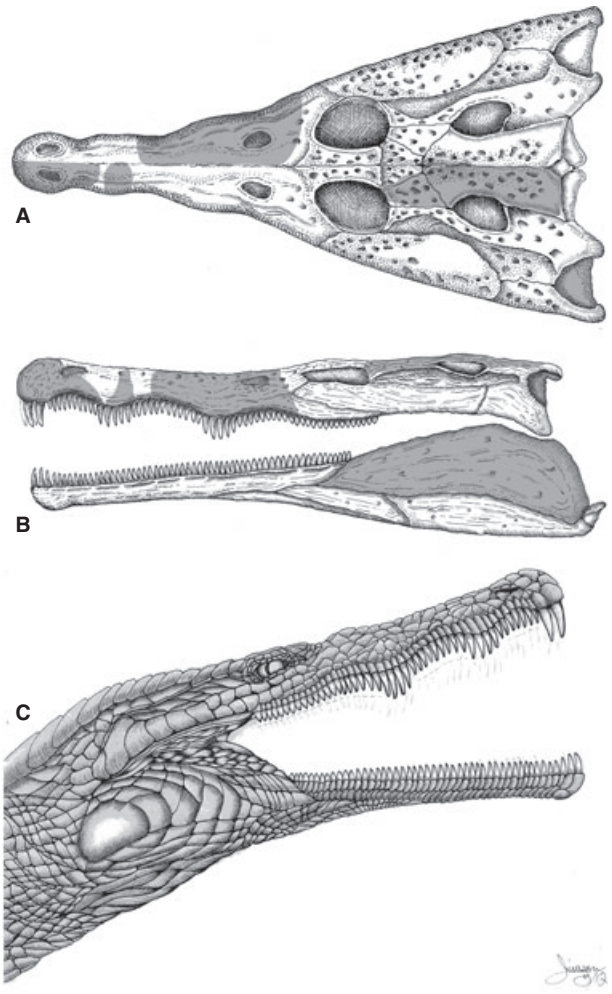

FIG. 6. Reconstructions of *Doswellia sixmilensis* based on the fossils described here, drawn by Pedro Toledo. A, B, skeletal reconstructions in A, dorsal and B, lateral views, with preserved elements shaded (right maxilla mirrored to left for lateral view). C, flesh reconstruction.

The new material we describe here also allows us to update the character scorings in two recent phylogenetic analyses incorporating *Doswellia* (Dilkes and Sues 2009; Desojo *et al.* 2011). Because Desojo *et al.* (2011) only added characters to Dilkes and Sues' (2009) analysis, all character numbers less than 86 we provide pertain to both analyses. Obviously, the presence of an antorbital fenestra changes the coding of this character (3) from 0 to 1. Not enough of the antorbital region is preserved to evaluate character 2, the presence of an antorbital fossa,

even with the redescription of this character provided by Desojo *et al.* (2011). Based on our interpretation of the premaxillary fragment, it retains the primitive state (0) with a downturned premaxillary tooth margin anteriorly (character 4; Fig. 2I, L). The external nares are not completely preserved, but, given our interpretation of the left premaxilla (Fig. 2I–L), we consider the nares to be marginal, not near the midline (character 5, state 1). Based on the preserved tooth and teeth fragments, we are confident that *Doswellia* teeth lack serrations composed of fine denticles (character 33, state 0). We note that existing crowns are only barely recurved, so Dilkes and Sues' (2009) coding of that character as the derived condition (1) apparently requires extremely little recurvature.

This allows us to improve the scoring of *Doswellia* from 39/85 (46 per cent) to 43/85 (51 per cent) of the characters in Dilkes and Sues' (2009) analysis. Because Desojo *et al.* (2011) only modified two characters of Dilkes and Sues (2009), neither of which we can score, then added 30 characters, most of which relate to the braincase or the appendicular skeleton, we are unable to score or rescore any of their modified or additional characters. Unfortunately, NMMNH P-61909 is too incomplete to provide insight into the several ambiguous potential synapomorphies of doswelliids enumerated by Desojo *et al.* (2011) based on other postcrania and skull characters. Additionally, we note that none of the characters we score here are known from the doswelliids *Tarjadia* or *Archeopelta*, so without new material of these taxa, a new doswelliid, or *Doswellia* itself, further tests of the monophyly and interrelationships of the Doswelliidae using the Desojo *et al.* (2011) character matrix are not possible.

BIOCHRONOLOGICAL SIGNIFICANCE

The genus *Doswellia* is now known from four lithostratigraphic units: (1) Falling Creek Formation of the Newark Supergroup in Virginia (type and referred material of *D. kaltenbachi*: Weems, 1980; Dilkes and Sues 2009); (2) the 'pre-Tecovas horizon of the Dockum Group' in West Texas as identified by Long and Murry (1995), which is the Colorado City Formation of the Chinle Group of our preferred lithostratigraphic terminology (Lucas *et al.* 1994); (3) Monitor Butte Formation of the Chinle Group in south-eastern Utah (Parrish 1999); and (4) the Bluewater Creek Formation of the Chinle Group in New Mexico, documented here.

The Falling Creek Formation of the Newark Supergroup is stratigraphically low in the basin fill of the Taylorsville basin in Virginia (Weems and Olsen 1997). Lucas and Huber (2003; Huber *et al.* 1993) regarded the tetrapod fossils from the Falling Creek Formation to be of Sanfordian (=Otischalkian) age and assigned this to the early Carnian based on palynostratigraphic and magnetostratigraphic correlations. Kozur and Weems (2010) reported conchostracan assemblages throughout the Falling Creek Formation that they assigned to their early Carnian *Laxitextella multireticulata* conchostracan zone. There thus is good agreement that the type and other referred material of *Doswellia kaltenbachi* from Virginia is of Otischalkian age.

In West Texas, the Colorado City Formation yields the tetrapod fossil assemblage used to define the Otischalkian LVF (Lucas and Hunt 1993; Lucas *et al.* 1993, 1994; Lucas 1998, 2010). Therefore, the *Doswellia* material from the Colorado City Formation documented by Long and Murry (1995) is of Otischalkian age. Long and Murry (1995, pp. 27, 29–33) assigned vertebral and osteoderm elements, TMM 31025-64, to either *Doswellia kaltenbachi* or *Doswellia*? This material was collected from the well-known *Trilophosaurus* quarry 1, described in Gregory (1945), which has yielded nearly complete skeletons of the archosauromorph *Trilophosaurus buettneri*. The osteoderms in TMM 31025-64 clearly pertain to *Doswellia*, however, some of the vertebral elements are reidentified here as belonging to *T. buettneri*. Indeed, the cervical vertebra illustrated by Long and Murry (1995, fig. 19n–r) shares the following characteristics with *T. buettneri*: keeled centrum, prominent groove on lateral surface of centrum between para- and diapophyses, and dorsal ridges on pre- and postzygapophyses forming an X-shape in dorsal view (see Spielmann *et al.*, 2007, 2008 for diagnoses and osteological descriptions of both *Trilophosaurus* species). Two of the dorsal vertebrae assigned to *D. kaltenbachi* by Long and Murry (1995, fig. 19F–M) bear a resemblance to the dorsal centra of *T. buettneri*, notably in that they lack a ventral keel. However, these two specimens are so fragmentary that definitive identification is difficult, though given the predominance of *T. buettneri* in the quarry (*c.* 95 per cent of identified specimens), assigning these vertebrae to *T. buettneri* is reasonable. The final vertebra illustrated by Long and Murry (1995, fig. A–E) as *D. kaltenbachi* has articulated rib fragments that do not match those of *T. buettneri* and thus may indeed pertain to *Doswellia*.

Parrish (1999) identified three osteoderms from the Upper Triassic near the Blue Lizard Mine in Red Canyon, Utah to Archosauriformes indet, but noted (p. 48) that they were most similar to *Doswellia*. Parrish (1999) hesitated to refer the Utah specimens to *Doswellia* because they lacked the nonpitted articular flange on the posterior margin and minor shape differences. However, these morphologies fall within the range of variation seen in the New Mexican osteoderms we describe here, so we consider the osteoderms to pertain to *Doswellia* sp. Parrish and Good (1987) and Parrish (1999) considered the Blue Lizard Mine assemblage to have been

derived from the Monitor Butte Member (=Formation of our usage). The Monitor Butte Formation is stratigraphically low in the Chinle Group section in south-eastern Utah, and it is a lithostratigraphic correlative of (homotaxial to) the Bluewater Creek Formation of north-western New Mexico-north-eastern Arizona (Lucas 1993; Lucas *et al.* 1997). The age of the Monitor Butte Formation, and its possible *Doswellia* record, is thus very likely Adamanian.

The relatively sparse vertebrate fauna of the Bluewater Creek Formation in west-central New Mexico has made biochronological determination difficult (Heckert 1997*a*, *b*, 2004; Heckert and Lucas 2002*a,* 2003). Nevertheless, based largely on fragmentary material of the aetosaurs *Stagonolepis* and *Desmatosuchus*, including the lost holotype of *Acompsosaurus wingatensis* Mehl *et al.* (1916), the Bluewater Creek Formation is of Adamanian age. The fragmentary osteoderm of the aetosaur *Tecovasuchus* also supports this hypothesis, as *Tecovasuchus* is an index taxon of the Adamanian (Heckert *et al.* 2007).

Thus, as Lucas (2010, p. 461) noted, *Doswellia* has records of both Otischalkian and Adamanian age. There appears to be a temporal succession of *Doswellia* species – Otischalkian *D. kaltenbachi* followed by Adamanian *D. sixmilensis*, named here. However, more species-level diagnostic specimens of *Doswellia* are needed before this can be a definite conclusion.

In 2002, we acquired samples of a tuffaceous sandstone at the base of the Blue Mesa Member locally and had the detrital zircons analysed by U-Pb geochronology, but were unable to report results until Heckert *et al.* (2009). Other workers have also obtained age estimates for this horizon, including Irmis and Mundil (2008) and Irmis *et al.* (2011) Despite using three different techniques, each at different laboratories, all have estimated an age of approximately 220 Ma (Table 1). As a detrital zircon estimate, this is by definition a maximum age, and the dated horizon is approximately 43 m above the *Doswellia* occurrence, so it is possible that the site is as much as several million years older than 220 Ma. However, given the rarity of Late Triassic age constraints associated with biostratigraphically useful tetrapods, *c.* 220 Ma is a reasonable approximation for the numerical age of the *D. sixmilensis* type locality, although it is several million years younger than the age estimates of homotaxial strata recently published by Ramezani *et al.* (2011). Recently, parties have argued that the Norian stage is much longer than previous thought (Furin *et al.* 2006), extending back to *c.* 228 Ma, which would indicate that *D. sixmilensis* is certainly Norian (and *D. kaltenbachi* likely so). However, there are real issues regarding the 'long Norian,' and Lucas *et al.* (2012) have recently documented biostratigraphic (palynomorph, conchostracan and tetrapod) evidence supporting retention of the Carnian–Norian boundary at *c.* 220 Ma, which would indicate that all known records of *Doswellia* are Carnian.

TABLE 1. Numerical age estimates for detrital zircons (maximum depositional age) for the base of the Blue Mesa Member above NMMNH locality 5700.

Age estimate	Methodology	Reference	System
219.6 ± 3.1 Ma	LA-ICP-MS	Heckert *et al.* (2009)	U-Pb
220.9 ± 0.6 Ma	ID-TIMS	Heckert *et al.* (2009)	U-Pb
218.7 ± 0.2 Ma	CA-TIMS	Irmis *et al.* (2011)	U-Pb

LA-ICP-MS, Laser ablation inductively plasma mass spectrometry; ID-TIMS, Ion dispersive thermal ionization mass spectrometry; CA-TIMS, Chemically abraded thermal ionization mass spectrometry.

CONCLUSIONS

The fossils we document here pertain to a new species of *Doswellia*, here named *Doswellia sixmilensis*. Re-evaluation of the known records of *Doswellia* indicates that the type species, *D. kaltenbachi*, and the holotype of *D. sixmilensis* are the only records that are diagnostic to species. Specimens assigned to *D. kaltenbachi* by Long and Murry (1995) are best considered *Doswellia* sp., except for the vertebrae, which probably pertain to *Trilophosaurus buettneri*. Isolated archosauriform osteoderms from Utah reported by Parrish (1999) probably do pertain to *Doswellia* but are not diagnostic below the species level. All records of *Doswellia* occur in strata traditionally considered Carnian, specifically the Otischalkian and Adamanian land-vertebrate faunachrons of Lucas and Hunt (1993). In addition to providing additional insight into the morphology of *Doswellia*, the new specimens provide a relatively rare unambiguous link, at the genus level, of a tetrapod taxon known from both the Newark Supergroup and the Chinle Group.

Acknowledgements. The fossil described here was discovered by S. Nesbitt in 2003 and collected with permission of the United States Forest Service through a permit obtained from the Cibola National Forest in July, 2004. Nesbitt and several volunteers of the NMMNH assisted in the excavation and volunteers R. Lindquist and J.B. Norton prepared the specimen. T. Culver at the UCM facilitated a loan to ABH to study the Utah specimens. A University Research Council Grant from Appalachian State University supported travel by ABH and the costs of the detrital zircon analyses of Heckert *et al.* (2009) in Table 1. Pedro Toledo executed the reconstructions in Figure 6. Reviews of a previous version of this paper by D. Dilkes and N. Fraser improved the content and expression of ideas presented here.

REFERENCES

ARCUCCI, A. and MARSICANO, C. A. 1998. A distinctive new archosaur from the Middle Triassic (Los Chañares Formation) of Argentina. *Journal of Vertebrate Paleontology*, **18**, 228–232.

BEATTY, B. L. and HECKERT, A. B. 2009. A large archosauriform tooth with multiple supernumerary carinae from the Upper Triassic of New Mexico (USA), with comments on carina development and anomalies in the Archosauria. *Historical Biology*, **21**, 57–65.

BRUSATTE, S. L., BENTON, M. J., LLOYD, G. T., RUTA, M. and WANG, S. C. 2011. Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **101**, 367–382.

CHATTERJEE, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London B*, **267**, 209–261.

DESOJO, J. B., EZCURRA, M. D. and SCHULTZ, C. L. 2011. An unusual new archosauriform from the Middle–Late Triassic of southern Brazil and the monophyly of Doswelliidae. *Zoological Journal of the Linnean Society*, **161**, 839–871.

DILKES, D. and SUES, H.-D. 2009. Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology*, **29**, 58–79.

FRASER, N. C. 2006. *Dawn of the dinosaurs: life in the Triassic*. Indiana University Press, Bloomington, 307 pp.

FURIN, S., PRETO, N., RIGO, M., ROGHI, G., GIANOLLA, P., CROWLEY, J. L. and BOWRING, S. A. 2006. High-precision U-Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology*, **34**, 1009–1012.

GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus*. *University of Texas Publication*, **4401**, 273–359.

HECKERT, A. B. 1997*a*. Litho- and biostratigraphy of the lower Chinle Group, east-central Arizona and west-central New Mexico, with a description of a new theropod (Dinosauria: Theropoda) from the Bluewater Creek Formation. Unpublished M. S. Thesis. University of New Mexico, Albuquerque, 278 pp.

—— 1997*b*. The tetrapod fauna of the Upper Triassic lower Chinle Group (Adamanian: latest Carnian), of the Zuni Mountains, west-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, **11**, 29–39.

—— 2004. Late Triassic microvertebrates from the lower Chinle Group (Otischalkian–Adamanian: Carnian), southwestern U.S.A. *New Mexico Museum of Natural History and Science Bulletin*, **27**, 1–170.

—— and LUCAS, S. G. 1999. A new aetosaur (Reptilia: Archosauria) from the Upper Triassic of Texas and the phylogeny of aetosaurs. *Journal of Vertebrate Paleontology*, **19**, 50–68.

—— —— 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie Teil **I 1998** Heft 11–12*, 1539–1587.

—— —— 2002*a*. Lower Chinle Group (Upper Triassic: Carnian) stratigraphy in the Zuni Mountains, west-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, **21**, 51–72.

—— —— 2002*b*. *Acaenasuchus geoffreyi* (Archosauria: Aetosauria) from the Upper Triassic Chinle Group: Juvenile of *Desmatosuchus haplocerus*. *New Mexico Museum of Natural History and Science Bulletin*, **21**, 205–214.

—— —— 2003. Triassic stratigraphy in the Zuni Mountains, west-central New Mexico. *New Mexico Geological Society Guidebook*, **54**, 245–262.

—— —— SPIELMANN, J. A. and HUNT, A. P. 2007. Biostratigraphic utility of the Upper Triassic aetosaur *Tecovasuchus* (Archosauria: Stagonolepididae), an index taxon of St. Johnsian (Adamanian: Late Carnian) time. *New Mexico Museum of Natural History and Science Bulletin*, **41**, 51–57.

—— —— DICKINSON, W. R. and MORTENSEN, J. K. 2009. New ID-TIMS U-Pb ages for Chinle Group strata (Upper Triassic) in New Mexico and Arizona, correlation to the Newark Supergroup, and implications for the 'long Norian'. *Geological Society of America Abstracts with Programs*, **41**, 123.

HUBER, P., LUCAS, S. G. and HUNT, A. P. 1993. Vertebrate biochronology of the Newark Supergroup Triassic, eastern North America. *New Mexico Museum of Natural History and Science Bulletin*, **3**, 179–185.

HUENE, F. VON. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt*, **65**, 268–275.

HUNGERBÜHLER, A. 2000. Heterodonty in the European phytosaur *Nicrosaurus kapffi* and its implications for the taxonomic utility and functional morphology of phytosaur dentitions. *Journal of Vertebrate Paleontology*, **20**, 31–48.

HUNT, A. P. 1989. Cranial morphology and ecology among phytosaurs. 349–354. *In* LUCAS, S. G., HUNT, A. P. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, 414 pp.

IRMIS, R. B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology*, **27**, 350–361.

—— and MUNDIL, R. 2008. New age constraints from the Chinle Formation revise global comparisons of Late Triassic vertebrate assemblages. *Journal of Vertebrate Paleontology*, **28**, 95A.

—— PARKER, W. G., NESBITT, S. J. and LIU, J. 2007. Early ornithischian dinosaurs: the Triassic record. *Historical Biology*, **19**, 3–22.

—— MUNDIL, R., MARTZ, J. W. and PARKER, W. G. 2011. High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. *Earth and Planetary Science Letters, Letters*, **309**, 258–267.

KAMMERER, C. F., NESBITT, S. J. and SHUBIN, N. H. 2012. The first silesaurid dinosauriform from the Late Triassic of Morocco. *Acta Palaeontologica Polonica*, **57**, 277–284.

KOZUR, H. W. and WEEMS, R. E. 2010. The biostratigraphic importance of conchostracans in the continental Triassic of

the northern hemisphere. *Geological Society, London, Special Publications*, **334**, 315–417.

LONG, R. A. and BALLEW, K. L. 1985. Aetosaur dermal armor from the Late Triassic of southwestern North America, with special reference to material from the Chinle Formation of Petrified Forest National Park. *Museum of Northern Arizona Bulletin*, **47**, 45–68.

—— and MURRY, P. A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History and Science Bulletin*, **4**, 254 p.

LUCAS, S. G. 1993. The Chinle Group: revised stratigraphy and biochronology of Upper Triassic strata in the western United States. *Museum of Northern Arizona, Bulletin*, **59**, 27–50.

—— 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **143**, 347–384.

—— 2010. The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology. 447–500. *In* LUCAS, S. G. (ed.). *The Triassic timescale*, Vol. 334. The Geological Society of London, London, 514 pp.

—— and HUBER, P. 2003. Vertebrate biostratigraphy and biochronology of the nonmarine Late Triassic. 143–191. *In* LETOURNEAU, P. M. and OLSEN, P. E. (eds). *The great rift valleys of Pangea in Eastern North America: sedimentology, Stratigraphy, and Paleontology*, Vol. 2. Columbia University Press, New York, 384 pp.

—— and HUNT, A. P. 1993. Tetrapod biochronology of the Chinle Group (Upper Triassic), western United States. *New Mexico Museum of Natural History and Science Bulletin*, **3**, 327–329.

———— and KAHLE, R. 1993. Late Triassic vertebrates from the Dockum Formation near Otis Chalk, Howard County, Texas. *New Mexico Geological Society, Guidebook*, **44**, 237–244.

—— ANDERSON, O. J. and HUNT, A. P. 1994. Triassic stratigraphy and correlations, southern High Plains of New Mexico–Texas. *New Mexico Bureau of Mines & Mineral Resources*, **150**, 105–126.

—— HECKERT, A. B., ESTEP, J. W. and ANDERSON, O. J. 1997. Stratigraphy of the Upper Triassic Chinle Group, Four Corners Region. *New Mexico Geological Society Guidebook*, **48**, 81–107.

—— TANNER, L. H., KOZUR, H. W., WEEMS, R. E. and HECKERT, A. B. 2012. The Late Triassic timescale: age and correlation of the Carnian–Norian boundary. *Earth-Science Reviews*, **114**, 1–18.

MARTZ, J. W. and SMALL, B. J. 2006. *Tecovasuchus chatterjeei*, a new aetosaur (Archosauria: Stagonolepididae) from the Tecovas Formation (Carnian, Upper Triassic) of Texas. *Journal of Vertebrate Paleontology*, **26**, 308–320.

MEHL, M. G., TOEPELMANN, W. C. and SCHWARTZ, G. M. 1916. New or little known reptiles from the Trias of Arizona and New Mexico with notes on the fossil bearing horizons near Wingate, New Mexico. *Bulletin of the University of Oklahoma*, **103**, 3–44.

NESBITT, S. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, **392**, 1–292.

—— SIDOR, C. A., IRMIS, R. B., ANGIELCZYK, K. D., SMITH, R. M. H. and TSUJI, L. A. 2010. Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature*, **464**, 95–98.

PARKER, W. G., IRMIS, R. B., NESBITT, S. J., MARTZ, J. W. and BROWNE, L. S. 2005. The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications of the diversity of early ornithischian dinosaurs. *Proceedings of the Royal Society of London, B*, **272**, 963–969.

PARRISH, J. M. 1999. Small fossil vertebrates from the Chinle Formation (Upper Triassic) of southern Utah. 45–50. *In* GILLETTE, D. D. (ed.). *Vertebrate paleontology in Utah*. Utah Geological Survey Miscellaneous Publication 99-1. Utah Geological Survey, Salt Lake City, 554 pp.

—— and GOOD, S. C. 1987. Preliminary report on vertebrate and invertebrate fossil occurrences, Chinle Formation (Upper Triassic), southeastern Utah. *Four Corners Geological Society*, **10**, 109–118.

RAMEZANI, J., HOKE, G. D., FASTOVSKY, D. E., BOWRING, S. A., THERRIEN, F., DWORKIN, S. I., ATCHLEY, S. C. and NORDT, L. C. 2011. High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. *Geological Society of America Bulletin*, **123**, 2142–2153.

SPIELMANN, J. A., LUCAS, S. G., HECKERT, A. B., RINEHART, L. F. and HUNT, A. P. 2007. Taxonomy and biostratigraphy of the Late Triassic archosauromorph *Trilophosaurus*. *New Mexico Museum of Natural History and Science Bulletin*, **40**, 231–240.

———— RINEHART, L. F. and HECKERT, A. B. 2008. The Late Triassic archosauromorph *Trilophosaurus*. *New Mexico Museum of Natural History and Science Bulletin*, **43**, 177 pp.

SUES, H.-D. 1992. A remarkable new armored archosaur from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology*, **12**, 142–149.

—— 2003. An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. *Canadian Journal of Earth Sciences*, **40**, 635–648.

—— and FRASER, N. C. 2010. *Triassic life on land – the great transition*. Columbia University, New York, 236 pp.

WEEMS, R. E. 1980. An unusual newly discovered archosaur from the Upper Triassic of Virginia, U.S.A. *Transactions of the American Philosophical Society*, **70**, 1–53.

—— and OLSEN, P. E. 1997. Synthesis and revision of groups within Newark Supergroup, eastern North America. *Geological Society of America Bulletin*, **109**, 195–209.